Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice.

Rusu, A ; Krackow, S

Abstract: Little is known about the behavioural mechanisms facilitating kin-preferential communal breeding in wild house mice (Mus domesticus). We evaluated the effect of kinship and male availability on aggression, social structure and reproductive skew in groups of female mice freely interacting and reproducing in seminatural indoor enclosures. Triplets of either sisters or nonsisters were established in enclosures provided with either one or three littermate males, which were unrelated and unfamiliar to the females. Sisters were more spatially associated and less aggressive than non-sisters, leading to higher incidences of communal breeding and reproduction. This is in agreement with theoretical considerations on kin selection in house mice. Reproductive success was highly skewed in favour of dominant females due to subordinate infertility or complete loss of first litters, which might have been caused by dominant females. In spite of this, subordinates only rarely dispersed from the enclosures, suggesting that perceived dispersal risk generally outweighed relatively reduced reproductive potentials. Aggression levels among females were significantly higher when one male was available, compared to when three males were available. We suggest that this might result from higher female-female competition for mates, due to the risk of missing fertilisation when synchronously oestrous females encounter limited numbers of males in a deme. Our results indicate that, first, communal nursing in house mice might have evolved to 'make the best out of a bad job' rather than to enhance offspring fitness; and, second, that female-female matecompetition might play an important role in shaping female social structure in this polygynous mammal.

DOI: https://doi.org/10.1007/s00265-004-0787-4

Originally published at:
Rusu, A; Krackow, S (2004). Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice. Behavioral Ecology and Sociobiology, 56(3):298-305.
DOI: https://doi.org/10.1007/s00265-004-0787-4

Behav Ecol Sociobiol (2004) 56:298–305
DOI 10.1007/s00265-004-0787-4

ORIGINAL ARTICLE

Alina S. Rusu · Sven Krackow

Kin-preferential cooperation, dominance-dependent reproductive skew, and competition for mates in communally nesting female house mice

Received: 13 August 2003 / Revised: 5 March 2004 / Accepted: 9 March 2004 / Published online: 14 April 2004

Abstract Little is known about the behavioural mechanisms facilitating kin-preferential communal breeding in wild house mice (*Mus domesticus*). We evaluated the effect of kinship and male availability on aggression, social structure and reproductive skew in groups of female mice freely interacting and reproducing in semi-natural indoor enclosures. Triplets of either sisters or non-sisters were established in enclosures provided with either one or three littermate males, which were unrelated and unfamiliar to the females. Sisters were more spatially associated and less aggressive than non-sisters, leading to higher incidences of communal breeding and reproduction. This is in agreement with theoretical considerations on kin selection in house mice. Reproductive success was highly skewed in favour of dominant females due to subordinate infertility or complete loss of first litters, which might have been caused by dominant females. In spite of this, subordinates only rarely dispersed from the enclosures, suggesting that perceived dispersal risk generally outweighed relatively reduced reproductive potentials. Aggression levels among females were significantly higher when one male was available, compared to when three males were available. We suggest that this might result from higher female-female competition for mates, due to the risk of missing fertilisation when synchronously oestrous females encounter limited numbers of males in a deme. Our results indicate that, first, communal nursing in house mice might have evolved to 'make the best out of a bad job' rather than to enhance offspring fitness; and, second, that female-female mate-competition might play an important role in shaping female social structure in this polygynous mammal.

Communicated by F. Trillmich

A. S. Rusu (✉) · S. Krackow
Zoologisches Institut,
Universität Zürich-Irchel,
Winterthurerstrasse 190, 8057 Zürich, Switzerland
e-mail: arusu@zool.unizh.ch
Tel.: +41-1-6355277
Fax: +41-1-6355490

Keywords Cooperative breeding · Kin competition · Social dominance · Female aggression

Electronic Supplementary Material Supplementary material is available in the online version of this article at http://dx.doi.org/10.1007/s00265-004-0787-4

Introduction

Communal breeding is a rare phenomenon in mammals (Hayes 2000), but has been observed regularly in commensal wild house mice (*Mus domesticus*) under laboratory conditions (Wilkinson and Baker 1988; Manning et al. 1992, 1995; König 1994b; Dobson et al. 2000; Dobson and Baudoin 2002), in semi-natural enclosures (Wilkinson and Baker 1988; Manning et al. 1992, 1995; König 1994b; Dobson et al. 2000; Dobson and Baudoin 2002), and occasionally in feral populations (Wilkinson and Baker 1988; Manning et al. 1992; Drickamer, personal communication). Commensal house mice often live in demes characterised by territorial defence polygyny (Lidicker 1976; Bronson 1979; Butler 1980; van Zegeren 1980; Singleton and Hay 1983; Wolff 1985; Gerlach 1990). Typically, demes consist of a territorial male, few or no subordinate males and several breeding, as well as non-breeding, females (Reimer and Petras 1967; Bronson 1979).

Within such demes, related females breed communally more often and more successfully than unrelated ones (Wilkinson and Baker 1988; Manning et al. 1992, 1995; König 1994b; Dobson et al. 2000; Dobson and Baudoin 2002). This is generally understood to reflect kin selection: while cooperative breeding would enhance individual female fitness due to synergistic effects on pup survival and development (König 1994a, 1994b), there is a high risk of deceptive behaviour leaving a female to invest in potentially unrelated offspring. Devaluation of deception costs due to inclusive fitness benefits when mothers are kin are then seen as allowing for the evolu-

tion of communal breeding in some species (Hayes 2000), including the house mouse.

Relationships within communal nests have been observed to be heavily skewed in terms of dominance and reproductive success in *Apodemus sylvaticus* (Gerlach and Bartmann 2002), and are not always egalitarian in wild house mice either (B. König, personal communication). Hence, it is not clear whether communal nursing of pups actually represents a mutualistic relationship, or whether one of the mothers actually benefits at the expense of the other(s).

Neither the behavioural mechanisms that facilitate communal breeding of kin in contrast to non-kin, nor the behavioural causes of reproductive skew among cooperating females, have been investigated to date. Therefore, we conducted detailed observations of behavioural development before and during communal nesting in groups of female house mice freely interacting and reproducing in semi-natural enclosures.

We compared social relationships and reproductive activities in groups of littermate females versus groups of unrelated and unfamiliar females, to investigate the effect of kinship. These female categories differ concomitantly in genetic relatedness and familiarity, i.e. we did not intend to separate genetic and familiarity effects on cooperative behaviour. However, full-sisters and unfamiliar non-sisters represent the most common female social categories that a maturing female will encounter in a natural house mouse deme (cf. Lidicker 1976; van Zegeren 1980; Gerlach 1990, 1996, 1998). We expected, therefore, that comparing these two categories would maximise our opportunity to observe evolved kin-differential behaviour, regardless of the proximate cause.

We also compared female agonistic relationships with either three or only one male available, assuming this to have profound consequences for female-female mate-competition. Indeed, in a preliminary experiment (Rusu and Krackow, unpublished data) we found that female aggression was significantly increased when the number of males available was experimentally decreased. Reproductive competition between females might indeed depend on male availability, although house mice are generally considered polygynous (Reimer and Petras 1967; Lidicker 1976; Pennycuik et al. 1986; Hurst 1987) and the potential for female-female competition might therefore be expected to be low. That is because it is well-known that females choose their mates according, for example, to their dominance status (Hayashi 1990; Drickamer 1992), or their genotypic quality, e.g. regarding MHC complement (Yamazaki et al. 1976) or t-haplotype (Lenington and Egid 1989). Moreover, females mated to preferred males produce more litters than females mated to non-preferred males, and the offspring from females mated with the preferred males showed enhanced social and reproductive performance (Drickamer et al. 2000). Hence, females in demes might compete for access to preferred males. Assuming that limitation of mating opportunity would strongly increase female-female competition, we expected female agonistic levels to differ with the number of males available in the enclosures, and also that this might have effects on social structure and/or communal breeding success.

Consequently, we evaluated the effects of kinship and male availability on aggression level, social structure and reproductive skew in groups of female house mice freely interacting and reproducing in semi-natural enclosures, to understand the development and determination of female reproductive alliance formation.

Methods

Animals and husbandry

Experimental animals (*M. domesticus*, 2*n*=24 chromosomes) were from litters of randomly bred, wild-caught to third-generation laboratory-outbred house mice, originating from three geographically separated wild populations in the vicinity of Zürich, Switzerland. Mice were kept in perspex Macrolon-cages (26.5×42×15 cm) under standard laboratory conditions (12:12 h light:dark cycle, lights on at 0600 hours, 22±1°C, 50–60% relative humidity). Pups were weaned at 21 days of age and placed into cages with same-sex littermates.

Enclosures and dispersal apparatus

Six enclosures (2×4 m, 60 cm sheet metal walls) were set up in an animal room subject to standard conditions, as above. Enclosures were filled with standard animal bedding and provided ad lib with food and water at four locations, with ten nest boxes, and compartmented by six 30-cm PVC-barriers (Fig. 1). When used more than once, enclosures and any devices were thoroughly cleaned with detergent and abundantly rinsed with water, and all bedding, food and water were replaced.

Each enclosure was fitted with a dispersal device that consisted of a water basin (80×40×30 cm, water level about 10 cm) connected by PVC tubes (5 cm diameter) to a hole in the enclosure and, at the opposite end, to a refuge laboratory cage. The cage contained food and water and thus allowed dispersers to stay (Fig. 1). Two triggerable devices automatically recorded time and the identity of

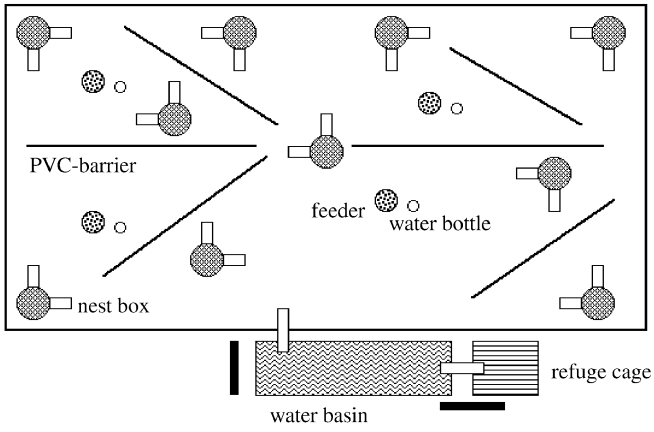

Fig. 1 Semi-natural enclosures were fenced using metal sheet walls (2×4×0.6 m), subdivided by PVC-barriers (30 cm in height) and provided with four feeding stations and 10 nest boxes. A closeable PVC-tube (5 cm diameter) led to a water basin (10 cm water level) with a refuge cage containing water and food pellets. At tube entries, animals were recorded with transponder readers (*bold bars*)

mice entering the connecting tube and refuge cage, by reading the transponders of the tagged mice (Fig. 1). Similar dispersal devices have successfully been used to study emigration in house mice (Gerlach 1990, 1996; Krackow 2003), and have recently been shown to accurately reflect natural dispersal behaviour (Nelson et al. 2002). Animals were considered dispersers if they remained in the dispersal cage for at least 24 h (i.e. at least one further night) without returning to the enclosure, when they were removed from the dispersal cage (i.e. from the experiment).

Experimental procedure

The experimental female triplets were either from one litter, i.e. females were littermate full-sisters (no litter provided more than one triplet), or were derived from three different breeding pairs, i.e., they were unfamiliar and unrelated. Males in each trial were always from different families than the females in the same trial and no litter yielded males to more than one trial. In a 2×2 factorial design, seven groups of three familiar full-sisters and seven groups of three unfamiliar, unrelated females were established, together with either one male (three sister groups and three non-sister groups) or three brothers (four sister groups and four non-sister groups). Since dominant male house mice show a low degree of tolerance towards same-sex subordinates, especially if they are unfamiliar (Reimer and Petras 1967; Lidicker 1976), we used littermate brothers to avoid fatal aggression. The males and females of each trial were simultaneously introduced into the enclosures, and they were allowed to freely interact during the whole experimental period. The day before introduction into the enclosures, animals were weighed, injected with Trovan transponders and marked with black dye (Rodol D; 1,4-phenylendiamine) for individual recognition.

For the first 2 weeks, agonistic and cohabitation data were recorded (see below). After 15 days, animals were provided with an opportunity to leave the enclosure, by connecting the dispersal apparatus (see above) for one week. During the following 5 weeks, we recorded any pregnancy and birth, noted nest position and attendance, and recorded the number of pups surviving to weaning. After termination of the experiments, females were sacrificed and dissected for uterine scars and number of embryos.

Data acquisition

Aggression

We observed the frequency of agonistic interactions during 30-min periods between 1800 and 2000 hours each day until day 15. Agonistic behaviours (attack, bite, chase, flee, approach/retreat, fight) were recorded following definitions in Mackintosh (1981). Behavioural sequences of repeated interactions were considered single behavioural events in the analyses.

The term ‘dominant’ has been used to describe the status of a consistent winner following repeated agonistic interactions without a rank reversal (Drews 1993). Binomial probabilities were calculated for deviation from equal number of wins and losses for each dyad. Relationships were judged unresolved when the binomial probability of the imbalance in dyadic wins and losses was above 5%. When we observed fewer than 0.5 agonistic interactions per hour over the whole period (13–15 half-hour observations), dyadic interactions were considered non-aggressive. Consistency of dominance order between the interacting individuals during the whole observation period was validated using the updated Elo-rating method (Albers and De Vries 2001). A rank reversal occurred in one dyad only (see Electronic Supplementary Material). In trials I and N, two females exhibited a clear hierarchical relationship while a third female did not interact aggressively sufficiently frequently to allow for a binomial test. According to the few interactions recorded (see Electronic Supplementary Material), for dominance rank analyses that females split rank with the subordinate in trial I and with the dominant in trial N.

Spatial association

We located animals daily during their resting period at midday for the whole experiment. From these data we calculated nest-use overlap as the percentage of co-use (associations) per total number of observations. To estimate the significance of dyadic association, we calculated the probability of occurrence in each particular nest box per individual for each dyad ($P1$, $P2$) and from that, we took the sum of the products $P1 \times P2$ per nest as the randomly expected probability of association (co-use of nest boxes). The one-sided binomial probability, using this expectation, for the observed or higher percentage overlap is given as a measure of dyadic association, and dyads were judged cohabiting for $P<0.05$.

Spatial association was calculated for the 15-day period before, and for the remaining time after, the dispersal phase, respectively. Hence, initial cohabitation measures dyadic association between nulliparous females prior to any maternal activity, while cohabitation after the dispersal phase incorporates communal breeding activity.

Reproduction

Litter size at birth was determined by counting the newly born pups at the daily inspections of nest-boxes. We assessed the number of uterine scars and embryos corresponding to each reproductive attempt by performing necropsy at the end of the experiment (Krackow 1992), updating the litter evaluations if necessary. Pregnancy sequences were estimated from dates of birth and from developmental stage of embryos at necropsy. From these data, reproductive ranks were calculated by assigning highest ranks to the female with the largest number of weaned pups. Also, we ranked the females that did not wean pups higher the earlier they achieved pregnancy (customising necropsy assessments where appropriate), and we assigned lowest rank to females not achieving pregnancy, including dispersing ones.

Statistical analyses

The effect of kin and male availability on female agonistic behaviour, as well as their interaction, was tested by using a general linear model ANOVA with ln-transformed number of aggressive events per hour and trial as the dependent variable. Transformation to natural logarithms of the Poisson-distributed event frequencies achieved a good fit of data (Shapiro-Wilk test of residuals from raw data analysis: $W=0.889$, $P=0.078$; transformed: $W=0.965$, $P=0.76$).

Data on individual incidences (e.g. occurrence of reproductive activity in a female) were compared between kin and male-availability trials using Generalized Linear Model (GLM; SAS 1989) analysis with logit-link functions and binomial error distribution (McCullagh and Nelder 1989). Dependency within trials was taken into account by scaling between-trial binomial variance according to Pearson’s GOF statistics (Krackow and Tkadlec 2001).

Trends with dominance rank were evaluated using the non-parametric S-statistics for monotonic trend of dependent data (Ferguson 1965, see also Krackow 2003). With $n=14$ trials and $k=3$ ranks, the standard normal deviate approximation ($z=S/\mathrm{SD}_S$) was used for significance determination (Ferguson 1965). Fisher’s exact probabilities are given for contingency tables involving binary characteristics of trials (e.g. double versus linear hierarchies depending on kin).

Results

Spatial association

While the number of available males did not affect female cohabitation patterns, remarkable differences occurred between sister and non-sister trials. All sisters except one

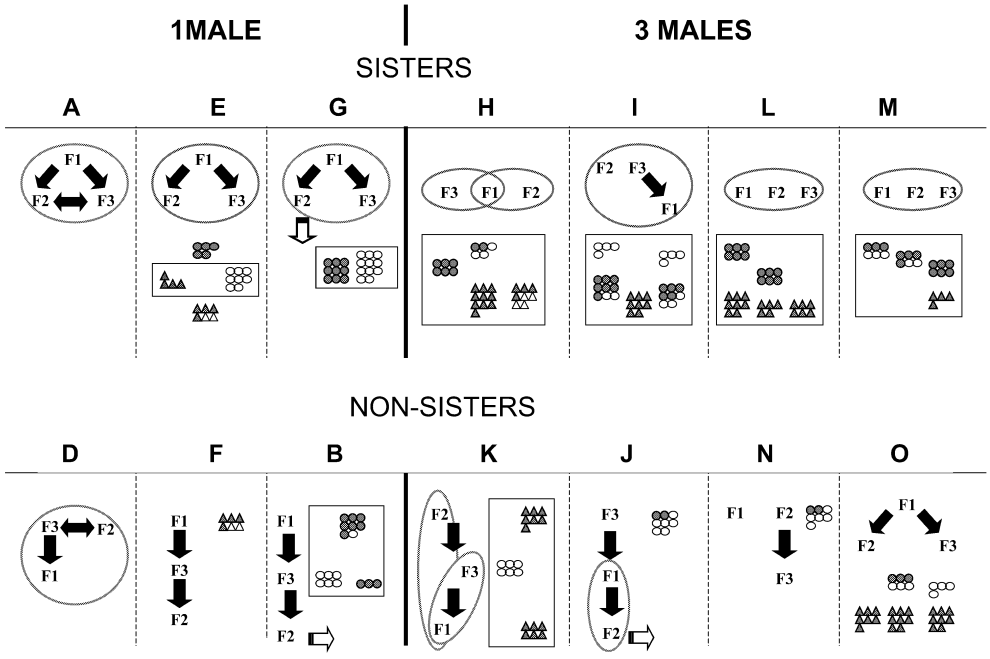

Fig. 2 Agonistic relationships, spatial association and reproductive outcomes in each experimental trial. *Black arrows* indicate dominance, *open* ones indicate dispersal. Linear hierarchies imply significant dominance of the dominant female over both subordinates. *Two-sided arrows* identify unresolved conflicts. Females initially cohabitating are *encircled*, communal breeders are surrounded by a *box*. *Filled circles* represent weaned pups, *open circles* represent lost ones, and *triangles* represent embryos found at necropsy. Distance of symbols from maternal acronyms, horizontal for linear hierarchies and vertical otherwise, maintain the temporal sequence of events. See Methods for detailed definitions of terms and Electronic Supplementary Material for original statistics

dyad exhibited significant spatial association during the first 15 days of the experiment before the dispersal phase (see Electronic Supplementary Material; Fig. 2). By contrast, in non-sisters only six of 21 dyads associated significantly in three out of seven trials (see Electronic Supplementary Material; Fig. 2). Hence, in five of the seven non-sister trials, non-cohabiting females were found, while there were none among sisters trials (Fisher's exact $P<0.03$, $n=14$). Three subordinate females (one in sister and two in non-sister trials) crossed the water barrier of the dispersal device (Fig. 2), and remained in the refuge cage during the subsequent 24 h until they were removed from the experiment. Most of the non-dispersing females visited the tube connecting the enclosure to the water basin for two to five nights during the dispersal phase, and hence they had information on the opportunity but did not disperse. Only two of the observed subordinate females were not recorded at the water basin entry.

Initially cohabiting females continued to share the nest after the dispersal phase with the exception of one dominant sister in trial E (Fig. 2). In three trials, one dyad in each that had not shown significant association during the initial phase nested communally thereafter (Fig. 2). Without exception, cohabiting females combined their litters within the same nest box. Non-cohabiting females used separate nest boxes for their litters in all cases. Hence, cooperative breeding patterns were highly congruent with initial cohabitation patterns. Accordingly, in the six reproductive trials of each kin group, non-sisters bred solitarily significantly more often than sisters (six out of 11 breeding non-sisters versus one out of 17 breeding sisters; GLM for the probability of breeding solitarily, kin: $F_{1,8}=7.33$, $P<0.03$, male availability: $F_{1,8}=1.51$, $P>0.25$, interaction: $F_{1,8}=2.24$, $P>0.17$).

Aggression and dominance

The level of inter-female aggression was significantly lower in three-male trials than in one-male trials (Fig. 3; $F_{1,10}=14.98$, $P<0.004$), and significantly lower between

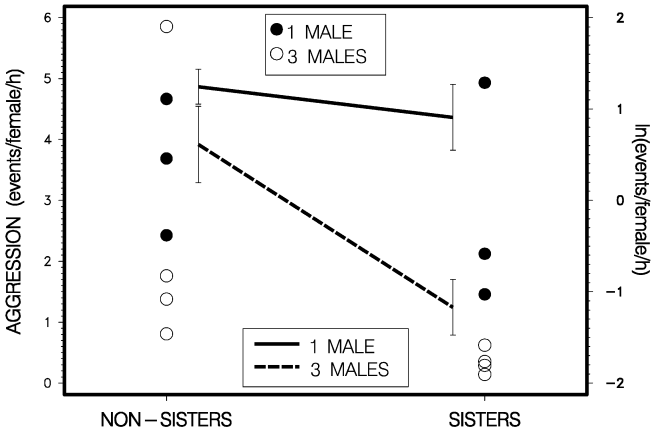

Fig. 3 Agonistic interactions per trial (*left axis*) and means±SE of ln-transformed values (*right axis*)

sisters than non-sisters ($F_{1,10}$=9.12, P<0.01). The interaction ($F_{1,10}$=4.26, P<0.07) indicated that the male availability-related difference in aggression was smaller in non-sisters than in sisters (Fig. 3).

In two trials (A, D), there was an unresolved conflict situation between two females with high levels of aggression (Fig. 2), preventing reproduction in those trials. Four out of five complete non-sister hierarchies were linear, i.e. one female significantly dominating the two others, of which the second ranked female dominated the third (see Electronic Supplementary Material; Fig. 2). In contrast, in one non-sister and all four sister trails exhibiting hierarchies, one female significantly dominated the other two, between which no or symmetrical amounts of aggression occurred (see Electronic Supplementary Material; Fig. 2; Fisher's exact P<0.05, n=9, for the difference in dominance structure between sisters and non-sisters triadic hierarchies). Body weight rank within trials at the start of the experiments appeared to promote dominance rank (Ferguson's trend test: z=1.91, P<0.06).

Reproductive performance

Pregnancy rates appeared to be higher among sisters than non-sisters and lower in the one-male than the three-male trials (Fig. 2; GLM for the occurrence of pregnant females, kin: $F_{1,10}$=4.41, P<0.07, male-availability: $F_{1,10}$=6.71, P<0.03, interaction: $F_{1,8}$=1.59, P>0.24). The male treatment effect was mainly due to the two trials with unresolved conflicts that prevented reproduction completely. Exclusion of those trials left only the kin effect being significant ($F_{1,10}$=5.27, P<0.046).

Reproduction was clearly skewed in favour of dominant females, as dominance rank significantly affected reproductive rank (Ferguson's trend test: z=2.38, P<0.02). Lower reproductive success in subordinates was not only due to lower fertility, because all dominant females became pregnant while five subordinates stayed infertile and three dispersed (excluding trials A and D; Fig. 2), but also due to reduced weaning success. Hence, all seven subordinate females that gave birth lost all young from their first litters, while all six dominant females that gave birth weaned at least part of their first litters (Fig. 2). All females from trials not exhibiting dominance hierarchies were reproductive, and none lost their first litters.

In all four communal breeding nests containing a dominant female, first litters of subordinate females preceded first breeding attempts of the dominant, while the five non-communally breeding dominant females were always the first to reproduce (Fig. 2; Fisher's exact P<0.01, n=9). Due to loss of first litters by subordinates, delayed dominants achieved highest reproductive ranks in all but one of the cases.

Discussion

Commensal house mouse females living in polygynous reproductive units (demes) often breed communally (König 1994b; Dobson et al. 2000; Dobson and Baudoin 2002), and kinship is known to facilitate female-female reproductive associations (Kareem and Barnard 1982, 1986; Wilkinson and Baker 1988; König 1989; Manning et al. 1995; Dobson et al. 2000). Our data show that familiar sisters cohabit significantly more often and are less aggressive towards each other than unfamiliar non-sisters before reproduction commences. As spatially associated females tended to subsequently breed communally, non-sisters bred solitarily significantly more often than sisters.

As stated earlier, our design was not intended to separate the proximate mechanism of kin discrimination, i.e. whether familiarity-dependent or genetic relatedness-dependent cues would actually translate into behavioural discrimination. However, genetically closely related females in a house mouse deme are generally familiar, and unfamiliar females will generally represent non-kin. Hence, discriminatory social behaviours between sister and non-sister groups should ultimately reflect kin selection processes.

Kin preferential cooperation

When wild house mouse females are paired experimentally, full-sisters achieve higher reproductive success than solitary females, while unrelated and unfamiliar females gain less (König 1993, 1994b). When given a choice in confined enclosures, unrelated and unfamiliar females appear to breed communally more rarely then sisters (Dobson et al. 2000; Hayes 2000). Also, field studies of feral house mice suggest that females living together are more likely to be related to one another than unrelated (Drickamer et al. 2003). The ultimate causation for this kin-dependent effect is not fully understood but, as mentioned in the Introduction, devalued costs of potential defection due to inclusive fitness benefits among kin are thought to be causal (Hayes 2000).

Our study suggests that defection risk does apply in house mice, as subordinate females lost their first litters, presumably due to infanticide or harassment by the dominant female. As subordinates continued to stay in the communal nest during lactation of pups of the dominant female, they might even endure further costs (which thereby benefit the dominant female) by engaging in nursing and/or other parental activities for the dominant female's pups. Thus, successfully raising the subordinate female's own pups appears to commence only at the second reproductive attempt. While we have no proof of maternal investment by the deceived female in the current experiment other than subordinate females' usage of the communal nest, other studies indicate that deceived mothers appear to stay maternally motivated and do indeed continue to invest in the other pups (B. König, personal communication). Communally breeding subor-

dinate sisters may more easily accept the disadvantages of reduced offspring survival and misdirected maternal investment because the dominant female's offspring are closely related to them, while non-sisters would raise non-kin. Hence, unrelated females would be expected to compete more severely, and more strongly avoid communal nests, in line with our findings.

Reproductive skew favouring social dominance

Females would increase their individual fitness if they deprived companion females in a deme of at least part of their reproductive success, a tactic well known to occur in group-living rodents, even among closely related females (Hoogland 1985). However, the evolutionary premium would be lower in sister groups than in non-sister ones, because such behaviour would reduce the inclusive fitness component of the depriving female. Accordingly, among sisters agonistic levels were significantly lower, subordinates did not establish clear hierarchies among themselves, and three socially and reproductively egalitarian groups emerged. These groups exhibited no significant amount of aggression, the females were all reproductive, and no loss of first litters was recorded.

Dominance among females as a measure of securing reproductive success has rarely been analysed in rodents, although it is well known that female aggression strongly limits productivity under over-crowded conditions in laboratory mouse groups (Lloyd 1975; Yasukawa et al. 1985; Chovnick et al. 1987; Parmigiani et al. 1989; Palanza et al. 1996; Chapman et al. 1998). Here, we present the first empirical evidence that body weight might determine agonistic dominance in unrelated wild house mouse females, a fact long established in males (van Zegeren 1980). Dominance, in turn, strongly increases reproductive success.

Though the behavioural mechanisms that translate agonistic dominance into reproductive skew could not be determined in our study, it eventually led to subordinate females staying infertile or losing all of their pups from first litters. Among female mammals, reproductive skew is frequently a consequence of subordinates being prevented from mating by the dominant females, either aggressively, as in *Suricata suricatta* (O'Riain et al. 2000), or *Mungos mungo* (Cant et al. 2001), or by pheromonal cues, as in *Heterocephalus glaber* (Faulkes et al. 1991). In the case of incomplete control of subordinate reproduction, dominant females might perform infanticide or attacks on the offspring, though such acts are rarely observed (Cant and Johnstone 1999). Given the high incidence of first litter loss, infanticidal behaviour of dominant females seems a plausible possibility in our study. However, dominants might risk losing their own offspring when committing infanticidal behaviour in communal nests, with pup discrimination being difficult (Cant 2000). This risk would be reduced if subordinate reproduction preceded dominant littering, concomitantly increasing subordinates' probability of staying in the nest due to induction of maternal motivation by giving birth (Noirot 1969). Hence, our finding that dominant females in communal nests always postpone reproduction after subordinate first littering might indicate a rather subtle behavioural endocrinological mechanism that allows dominant mothers to exploit subordinate co-breeders while avoiding impairment of their own reproduction. Clearly, further research on this topic seems highly warranted.

A cruel bind for subordinates

Although the preceding argument suggests that subordinates suffer great disadvantages in terms of reproductive success, only three of them dispersed. Clearly, perceived dispersal risk must have outweighed reduced expected fitness for most subordinates. Given high mortality rates during dispersal under natural conditions, staying in a thriving deme and waiting for a reproductive opportunity is suggested as a successful strategy in house mice (Gerlach 1990). Occasional reproduction in communal or solitary nests, as observed in our study, may further increase the dispersal threshold.

Competition for males

The level of female aggression was significantly higher with only one male available than with three males available, between sisters as well as non-sisters. This effect appeared to be more pronounced in non-sisters, and overall aggression level was lower in sisters. Here, we argue that this effect could result from female-female competition for males.

In house mice, mating behaviour involves variable numbers of copulatory sequences, each consisting of multiple intromissive mountings, of variable duration and frequency, which usually end up with ejaculation (Dewsbury 1979). Mating often continues over a whole night until males eventually produce a vaginal plug at final ejaculation, presumably when the 6–18 h female oestrus period is about to end. Plug formation is known to hinder further fertilisation for several hours (De Catanzaro 1991), indicating that sperm competition plays a major role in house mouse mating behaviour evolution.

In spite of the substantial temporal extent of mating sequences, fertilisation success appears not to depend on any measure of male mating efforts in wild house mice under laboratory conditions (Dewsbury 1972). However, female mice appear to be actively promiscuous as they usually switch partners after the first ejaculation when access to multiple mates is provided in experimental settings (Eklund 1997; Rolland et al. 2003). Moreover, females move freely across male territories and actively approach the territorial males under more natural conditions (Reimer and Petras 1967; Lidicker 1976; Wolff 1985; Pennycuik et al. 1986).

In the light of female promiscuous behavioural tendency and intense sperm competition, extended mating

sequences would give males a competitive advantage by depositing increased amounts of sperm as well as occupying female oestrous time as a form of mate guarding (cf. Rolland et al. 2003). Consequently, until plug formation, males might have limited potential to simultaneously engage in copulatory behaviour with additional females. Obviously, in case there were more females in oestrus than males available there would be a risk of not being fertilised, as oestrus in supernumerary females might have ended before fertile males become available. Accordingly, in laboratory mice fertility decreased with female-biased mating ratios (Krackow 1997). Clearly, female-female competition for mates would follow in demes with three females and only one male present, given that the probability of synchronous oestrus in a male-induced oestrus cycle of several females approaches 50% (Whitten 1956).

If our argument on the temporal extension of mating sequences is correct, male behaviours that evolved due to male-male competition in the promiscuous house mouse mating system would ultimately cause female competition for mates.

Conclusions

Kinship decreased levels of solitary breeding and agonistic competition, and increased reproductive success, among female house mice in our semi-natural enclosures, while competition for mates increased agonistic interactions and decreased female reproductive success. This is in congruence with adaptive expectation, as deception risk in communal nests would pose lower costs on related females due to inclusive fitness advantages, and limited availability of fertile males would indeed pose a risk of infertile oestrus in house mouse demes. Clearly, striving for social dominance paid off in terms of heavily skewed reproductive success in favour of dominant females. In spite of this, subordinate females dispersed only rarely from the enclosures, which might indicate that fitness loss due to dispersal is generally higher than restricted reproductive output in a subordinate position. This leaves open the question of whether communal nursing would actually occur in nature without any serious environmental constraint on dispersal, at least among non-relatives. In the absence of studies, whether observational or experimental, that are void of severe restrictions on the reproductive options of females, the question of whether communal nursing evolved due to an enhanced fitness when compared to solitary breeding, or to ‘make the best out of a bad job’, should be re-addressed in future studies.

Acknowledgements We thank Barbara König, Lee Drickamer, Alan McElligott and three anonymous reviewers for many useful comments on the manuscript. This research was funded by the Swiss National Foundation (SNF; no. 31-59609.99): Support to S.K. was granted by the German Research Council (DFG; KR1290/6). Animal experimentation was approved by the Swiss Animal Experimentation Commission (Kantonale Tierversuchskommission; no. 164/99).

References

Albers PCH, De Vries H (2001) Elo-Rating as a tool in the sequential estimation of dominance strenghts. Anim Behav 61:489–495

Bronson FH (1979) The reproductive ecology of the house mouse. Q Rev Biol 54:265–299

Butler RG (1980) Population size, social behaviour, and dispersal in house mice: a quantitative investigation. Anim Behav 28:78–85

Cant MA (2000) Social control of reproduction in banded mongooses. Anim Behav 59:147–158

Cant MA, Johnstone RA (1999) Costly young and reproductive skew in animal societies. Behav Ecol 10:178–184

Cant MA, Otali E, Mwanguhya F (2001) Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). J Zool 254:155–162

Chapman JC, Christian JJ, Pawlikowski MA, Michael SD (1998) Analysis of steroid hormone levels in female mice at high population density. Physiol Behav 64:529–533

Chovnick A, Yasukawa NJ, Monder H, Christian JJ (1987) Female behavior in populations of mice in the presence and absence of male hierarchy. Aggressive Behav 13:367–375

De Catanzaro D (1991) Duration of mating relates to fertility in mice. Physiol Behav 50:393–395

Dewsbury DA (1972) Patterns of copulatory behavior in male mammals. Q Rev Biol 47:1–33

Dewsbury DA (1979) Pregnancy and copulatory behavior in random-bred house mice mated in postpartum estrus. Bull Psychonom Soc 13:320–322

Dobson FS, Baudoin C (2002) Experimental tests of spatial association and kinship in monogamous mice (*Mus spicilegus*) and polygynous mice (*Mus musculus domesticus*). Can J Zool 89:980–986

Dobson FS, Jacquot C, Baudoin C (2000) An experimental test of kin association in the house mouse. Can J Zool 78:1806–1812

Drews C (1993) The concept and definition of dominance in animal behaviour. Behaviour 125:283–313

Drickamer LC (1992) Oestrus female house mice discriminate dominant from subordinate males and sons of dominant from sons of subordinate males by odour cues. Anim Behav 43:869–870

Drickamer LC, Gowaty PA, Holmes CM (2000) Free female mate choice in house mice affects reproductive success and offspring viability and performance. Anim Behav 59:371–378

Drickamer LC, Wagner DM, Robinson AS (2003) Double captures of house mice (*Mus musculus*) with information on genetic relatedness. Am Mid Nat 150:308–320

Eklund A (1997) The major histocompatibility complex and mating preferences in wild house mice (*Mus domesticus*). Behav Ecol 8:630–634

Faulkes CG, Abbott DH, Jarvis JUM (1991) Social suppression of reproduction in male naked mole-rats, *Heterocephalus glaber*. J Reprod Fertil 91:593–604

Ferguson GA (1965) Nonparametric trend analysis. McGill University Press, Montreal

Gerlach G (1990) Dispersal mechanisms in a captive wild house mouse population (*Mus domesticus* Rutty). Biol J Linn Soc Lond 41:271–277

Gerlach G (1996) Emigration mechanisms in feral house mice—a laboratory investigation of the influence of social structure, population density, and aggression. Behav Ecol Sociobiol 39:159–170

Gerlach G (1998) Impact of social ties on dispersal, reproduction and dominance in feral house mice (*Mus musculus domesticus*). Ethology 104:487–499

Gerlach G, Bartmann S (2002) Reproductive skew, costs, and benefits of cooperative breeding in female wood mice (*Apodemus sylvaticus*). Behav Ecol 13:408–418

Hayashi S (1990) Social condition influences sexual attractiveness of dominant male mice. Zool Sci 7:889–894

Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. Anim Behav 59:677–688
Hoogland JL (1985) Infanticide in prairie dogs: lactating females kill offspring of close kin. Science 230:1037–1040
Hurst JL (1987) Behavioural variation in wild house mice *Mus domesticus* Rutty: a quantitative assessment of female social organization. Anim Behav 35:1846–1857
Kareem AM, Barnard CJ (1982) The importance of kinship and familiarity in social interactions between mice. Anim Behav 30:594–601
Kareem AM, Barnard CJ (1986) Kin recognition in mice—age, sex and parental effects. Anim Behav 34:1814–1824
König B (1989) Behavioural ecology of kin recognition in house mice. Ethol Ecol Evol 1:99–100
König B (1993) Maternal investment of communally nursing female house mice (*Mus musculus domesticus*). Behav Proc 30:61–74
König B (1994a) Communal nursing in mammals. Verh Dtsch Zool Ges 87:115–127
König B (1994b) Fitness effects of communal rearing in house mice. The role of relatedness versus familiarity. Anim Behav 48:1449–1457
Krackow S (1992) Sex ratio manipulation in wild house mice: The effect of fetal resorption in relation to the mode of reproduction. Biol Reprod 47:541–548
Krackow S (1997) Effects of mating dynamics and crowding on sex ratio variance in mice. J Reprod Fertil 110:87–90
Krackow S (2003) Motivational and heritable determinants of dispersal latency in wild male house mice (*Mus musculus musculus*). Ethology 109:671–689
Krackow S, Tkadlec E (2001) Analysis of brood sex ratios. Behav Ecol Sociobiol 50:293–301
Lenington S, Egid K (1989) Environmental influences on the preferences of wild female house mice for males of differing t-complex genotypes. Behav Genet 19:257–266
Lidicker WZ (1976) Social behaviour and density regulation in house mice living in large enclosures. J Anim Ecol 45:677–697
Lloyd JA (1975) Social structure and reproduction in two freely-growing populations of house mice (*Mus musculus* L.). Anim Behav 23:413–424
Mackintosh JH (1981) Behaviour of the house mouse. Symp Zool Soc Lond 47:337–365
Manning CJ, Dewsbury DA, Wakeland EK, Potts WK (1995) Communal nesting and communal nursing in house mice, *Mus musculus domesticus*. Anim Behav 50:741–751
Manning CJ, Wakeland EK, Potts WK (1992) Communal nesting patterns in mice implicate MHC genes in kin recognition. Nature 360:581–583
McCullagh P, Nelder JA (1989) Generalized linear models, vol 37, 2nd edn. Chapman and Hall, London
Nelson AR, Johnson CL, Matter WJ, Mannan RW (2002) Tests of emigration in small mammals under experimental conditions. Can J Zool 80:2056–2060
Noirot E (1969) Serial order of maternal responses in mice. Anim Behav 17:547–550
O'Riain MJ, Bennett NC, Brotherton PNM, McIlrath G, Clutton-Brock TH (2000) Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (*Suricata suricatta*). Behav Ecol Sociobiol 48:471–477
Palanza P, Re L, Mainardi D, Brain PF, Parmigiani S (1996) Male and female competitive strategies of wild house mice pairs (*Mus musculus domesticus*) confronted with intruders of different sex and age in artificial territories. Behaviour 133:863–882
Parmigiani S, Mainardi M, Brain PF, Haug M, Brunoni V (1989) Variation in aggressive behavior and anatomo-physiological correlates generated by crowding without physical contact in the house mouse. Aggressive Behav 15:191–200
Pennycuik PR, Johnston PG, Westwood NH, Reisner AH (1986) Variation in numbers in a house mouse population housed in a large outdoor enclosure: seasonal fluctuations. J Anim Ecol 55:371–379
Reimer JD, Petras ML (1967) Breeding structure of the house mouse, *Mus musculus*, in a population cage. J Mammal 48:88–99
Rolland C, Macdonald DW, De Fraipont M, Berdoy M (2003) Free female choice in house mice: leaving best for last. Behaviour 140:1371–1388
SAS (1989) SAS/STAT User's guide: version 6. SAS Institute, Cary, N.C.
Singleton GR, Hay DA (1983) The effect of social organization on reproductive success and gene flow in colonies of wild house mice, *Mus musculus*. Behav Ecol Sociobiol 12:49–56
Whitten WK (1956) Modification of the oestrous cycle of the mouse by external stimuli associated with the male. J Endocrinol 13:399–404
Wilkinson GS, Baker MAE (1988) Communal nesting among genetically similar house mice. Ethology 77:103–114
Wolff RJ (1985) Mating behavior and female choice: their relation to social structure in wild caught house mice (*Mus musculus*) housed in a semi-natural environment. J Zool (Lond) 207:43–51
Yamazaki K, Boyse EA, Mike V, Thaler HT, Mathieson BJ, Abbott J, Boyse (1976) Control of mating preferences in mice by genes in the major histocompatability complex. J Exp Med 144:1324–1335
Yasukawa NJ, Monder H, Leff FR, Christian JJ (1985) Role of female behavior in controlling population growth in mice. Aggressive Behav 11:49–64
Zegeren K van (1980) Variation in aggressiveness and the regulation of numbers in house mouse populations. Neth J Zool 30:635–770